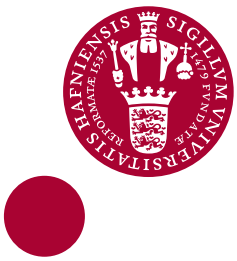

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Postdisperzní predace semen lesních dřevin limituje opětovnou kolonizaci lesních výsadeb na bývalé orné půdě

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Reforestation of ex-arable land in temperate regions increases the area of potential habitat for forest plants. However, the herbaceous plant layer of these plantations contains fewer forest species than comparable plantations at continuously forested sites. One of the reasons for this might be differences in recruitment. The present study addresses post-dispersal seed predation, mainly of woody plants, as the factor limiting the recolonization of young oak plantations in southern Sweden. Our objectives were to investigate differences in dispersal and post-dispersal seed predation between first-generation forest plantations on ex-arable land and re-planted clear-cuts on continuously forested land. There was no recruitment following the experimental sowing of six common woody species (*Alnus glutinosa*, *Betula pendula*, *Frangula alnus*, *Sambucus nigra*, *Sorbus aucuparia* and *Sorbus intermedia*). Thus, the colonization of forest plantations by native shrubs and trees appears to be habitat-limited; the only exception being *Rhamnus catharticus*, for which poor dispersal ability may be more important. Post-dispersal seed predation of forest shrubs and trees was marked, especially in relatively small and isolated plantations on ex-arable land. There was a high seed predation of *Crataegus monogyna*, *Sorbus aucuparia* and *Viburnum opulus* on ex-arable land, while that of *Frangula alnus* and *Sambucus racemosa* was not associated with site placement and land-use history. Seed predation is probably a more important factor limiting restoration of near-natural forests than previously thought.

K e y w o r d s: deciduous forest, dispersal ability, forest restoration, habitat limitation, land-use history, species richness.

Introduction

Human population expansion in the pre-industrial era and the consequent conversion of land to agriculture strongly reduced the original area of deciduous forest in Europe and North America (Flinn & Vellend 2005). Consequently, the area of habitat for species dependent on these ecosystems was strongly reduced and fragmented. More recently, however, increasing demands for forest products, ecosystem services and conservation of biodiversity have led to reforestation. In Europe, reforestation has mainly involved planting

tree saplings on what was previously arable land (Mather 2001). Thus, the area potentially suitable for forest-inhabiting species has been enlarged. However, it is questionable whether planting trees is an effective means of restoring forest biodiversity. Empirical data suggest that forest organisms generally colonize such plantations very slowly. This is especially true of vascular plants. The herbaceous plant layer in plantations on ex-arable land consists of fewer forest species than in old-growth forests (e.g. Honnay et al. 1999a, Graae et al. 2004b, Flinn & Vellend 2005), and fewer species than in similar-aged plantations at continuously forested sites (Gachet et al. 2007, Valtinat et al. 2008). Some species of herbaceous plants appear to be more specialized in the sense that they do not occur in recent forests (Wulf 1997, Honnay et al. 1998). Much less is known about the recolonization by species of shrubs and trees, although McEuen & Curran (2006) report an inverse relationship between the richness in woody plant species and the increasing isolation of plantations in an arable matrix. The composition of the herbaceous plant and shrub layers has direct influence on the forest fauna, in particular invertebrates (Fayt et al. 2006, Tyler 2008). It is also an important determinant of the recreational value of forest plantations (Koch & Jensen 1988: p. 305). Thus, the slow recolonization of new forests by herbaceous and woody plants is of concern for forest restoration, in terms of biodiversity management, ecosystem services and amenity.

Slow recolonization of recent plantations by forest plants raises questions about the possible causes. Absence of plant species in a forest may result from chance-related dispersal processes (dispersal limitation) and/ or local filtering by the biotic and abiotic environment (habitat limitation, sensu Eriksson & Ehrlén 1992). The relative importance of these two processes is best investigated by sowing seeds of target species at sites where the species is absent and by comparing seedling emergence in experimental and control plots (Münzbergová & Herben 2005, Clark et al. 2007). Poor dispersal of propagules into unoccupied suitable sites has been demonstrated for herbaceous forest plants (Eriksson & Ehrlén 1992, Verheyen et al. 2003a, Graae et al. 2004a, Ehrlén et al. 2006). A recent review (Clark et al. 2007) indicates that seed limitation is more important than habitat limitation for forest than grassland plants. So far, few studies have considered woody species, but McEuen & Curran (2004) report that the lack of woody species in forest fragments is mainly a consequence of poor dispersal.

Differences in the dispersal of species may be attributed to differences in dispersal ability. Species with wind-dispersed minute seeds or spores are often fast colonizers, while myrmecochores are much slower colonizers and species dispersed by vertebrates occupy an intermediate position (Matlack 1994, Brunet & von Oheimb 1998, Graae 2000, 2002, Mouissie et al. 2005). For vertebrate-dispersed forest species, animal behaviour may be dependent on the landscape matrix and degree of forest fragmentation, which may modify seed shadows and limit dispersal (Haas 1995, Higgins et al. 2003, Russo et al. 2006, Bailey 2007).

A number of factors may prevent the successful recruitment from propagules that arrive at a site. Seed addition experiments cannot, however, distinguish between the many possible underlying abiotic and biotic causes of habitat limitation. Lack of recruitment may occur due to post-dispersal seed predation, which in turn may have a different effect depending on the species of plant. Size and shape of seeds may have a major influence on the risk of seed predation (Kollmann et al. 1998), partly because these attributes affect the attractiveness of seeds as food, partly because they are key factors in determining the

depth in the soil at which the seed is buried (Hulme & Borelli 1999, Saatkamp et al. 2009). Land-use history and forest configuration in the landscape are likely to influence seed predation patterns via the population densities of seed-eating insects and mammals. Seed predators may be forest-specific, and hence themselves constrained by colonization ability, or they may be more abundant in the landscape matrix and thus more likely to affect plant recruitment in isolated stands and near forest margins (Kollmann & Buschor 2003). Habitat limitation may also be caused by constraints on seed germination and seedling emergence, such as soil conditions and the presence of a litter layer, or competition with established vegetation. All these obstacles may vary due to differences in land-use history.

Several investigations have revealed elevated phosphorus levels in the soils of abandoned arable land and that these high levels can persist for decades (Honnay et al. 1999b, Verheyen et al. 1999, Garz et al. 2000, Dupouey et al. 2002). Moreover, abandoned arable land often has a higher soil pH and lower organic content than continuously forested sites, due to fertilization, harvesting of crops and higher mineralization rates. Although such differences influence the diversity of forest plants (e.g. Verheyen & Hermy 2001, Verheyen et al. 2003b, De Keersmaeker et al. 2004, Valtinat et al. 2008), they do not necessarily determine whether forest plants will become established (Graae et al. 2004a, Valtinat et al. 2008). A dense litter layer, which can potentially impede root and shoot penetration, may be less common in plantations on ex-arable land. The herbaceous plant layer in forest plantations on ex-arable land or isolated forest patches may contain more competitive species of plants as a legacy of former land-use or due to greater influx of weed seeds from the surroundings. This has in some cases resulted in a recruitment of fewer forest plants in recent plantations on ex-arable sites or isolated forests (Verheyen & Hermy 2001).

The present study has two objectives: (i) to explore dispersal and habitat limitation of forest shrubs and trees by sowing seed, and (ii) to investigate the importance of post-dispersal seed predation as a factor of habitat limitation. Throughout, first-generation forest plantations on ex-arable land are compared with similar-aged plantations in clear-cuts on continuously forested land.

Materials and methods

Study area

This study was done at Skåne (Scania) in the southernmost province of Sweden (55°32'N, 13°11'E), which has a cool-temperate climate. The study area, encompassed within the estates of Skabersjö and Torup, is dominated by deciduous forests, probably the natural vegetation, and arable land (Brunet 2007). In southern Sweden, the planting of new deciduous stands of trees on former agricultural fields has been encouraged since the 19th century. During the period 1920–1960, a number of oak stands were planted, either on abandoned arable fields or in clear-cuts on previously forested land (hereafter referred to as 'ex-arable land' and 'continuously forested land'); some of the forest lots are embedded in intensively used agricultural land. The continuously forested land has a documented history of forest being present during the past 300 years (Brunet 2007), but may be for longer.

At the time the ex-arable fields were abandoned, cultivation consisted of ploughing, application of manure, liming and harvesting. The addition of lime probably began in the early 19th century. Differences in soil properties between ex-arable and continuously

forested land are relatively persistent and include higher pH, higher total nitrogen (higher nitrate, lower ammonium) mineralization rate and lower moisture content during summer, with the greatest differences in the top soil (Valtinat et al. 2008). Herbaceous vegetation differs between land-use types as well, with more arable weeds in the forests on ex-arable land and some true forest species confined to continuously forested sites. However, a number of well-dispersed acid-sensitive forest plants are found more often in forests on ex-arable land than in areas that have been continuously forested (Valtinat et al. 2008). Data on canopy cover, soil pH, soil ammonium and nitrate mineralization rates were obtained from the same study.

Site selection

Based on data on land-use history and plantation age, 12 plantations were selected for investigation, six on continuously forested land adjacent to ancient forest (age 48–68 years, stand area 0.8–6.7 ha) and six on ex-arable land (age 45–69 years, stand area 1.0–3.1 ha; site characteristics in Appendix 1). The ex-arable plantations were adjacent to agricultural fields, pasture and, in some cases, secondary forest stands. The stands on continuously forested land were completely embedded in a forest matrix, except one that had a field on one side. All stands had a canopy of pedunculate oak (*Quercus robur* L.) mixed with some sycamore (*Acer pseudoplatanus* L.), beech (*Fagus sylvatica* L.) and birch (*Betula pendula* L.). Canopy cover was on average 63%, and soil pH (H_2O) was 3.8±0.4. In each of the 12 stands, one quadrat of 25 × 20 m^2 on a well-drained level area was selected and marked with permanent markers. Information on stand area and age, total forest area and distance to the nearest ancient forest was obtained from maps in a GIS environment. In each plot, spontaneous regeneration of woody plants was recorded quantitatively (percentage cover) in ten subplots of 1 × 1 m^2 placed systematically. Saplings were scored in one of two height categories (< 1 m and 1–5 m).

Experimental sowing of woody plants

A 2 × 3 m experimental plot was placed centrally in each quadrat and divided into six 1-m^2 subplots. In April 2005, two subplots were subjected to a small-scale disturbance, i.e. removal of all above-ground vegetation, leaf litter and the upper 5 cms of soil. Experimental sowing of seeds was combined with the small-scale disturbance in the following way: (i) no biomass or litter removed and seed sprinkled over the litter and vegetation; (ii) no biomass or litter removed and seeds sown below the litter and vegetation, in order to conceal them and to ensure direct contact with the soil below; and (iii) complete removal of above-ground vegetation, leaf litter and the upper 5 cms of soil and sowing of seeds at a depth of approximately 1 cm. In each pair of treatment subplots, one was sown and the other left as a control to record background seedling emergence in each disturbance regime.

The species sown were *Alnus glutinosa* (L.) Gaertn., *Betula pendula* Roth, *Frangula alnus* Mill., *Rhamnus catharticus* L., *Sambucus nigra* L., *Sorbus aucuparia* L. and *Sorbus intermedia* (Ehrh.) Pers. These species are relatively common in the study area and occur spontaneously in young forest plantations (Tyler et al. 2007). Stratified seeds were obtained from Björkhaga nursery, Veberöd. In the nursery, all these species germinated well and reached full germination within a few months. Ten seeds per species per subplot were sown in April 2005. Experimental plots were visited at approximately monthly intervals

and the final number of seedlings was recorded in August 2006. By surveying seedling emergence over two summers, the possibility that seeds entered secondary dormancy after sowing and remained viable in the soil was ruled out.

Seed predation experiment

Five species of woody plants with fleshy fruits, *Crataegus monogyna* Jacq., *Frangula alnus* Mill., *Sambucus racemosa* L., *Sorbus aucuparia* L. and *Viburnum opulus* L. were selected for a seed predation experiment. These are among the most common woody species with fleshy fruits in the forests studied. *Crataegus laevigata* (Poir.) DC., *Prunus spinosa* L. and *Sambucus nigra* L. are also quite common. *Crataegus laevigata* is, however, very similar to *C. monogyna*, *Prunus spinosa* with fruit ripening in winter and *Sambucus nigra* is considered to be a ruderal species as it occurs exclusively in isolated wood-lots on ex-arable land and was therefore excluded. As a control for the five woody species, one herbaceous species was used, i.e. *Carex sylvatica* Huds., which has nutlets enclosed in utricles. All seeds for the predation experiment were collected in the study area. Each species was collected from one site, but from a number of mother plants. For *Crataegus monogyna*, whole fruits were used because it was difficult to remove the flesh of the fruits, whereas for the other fleshy-fruited species, seeds were extracted from the fruit flesh by crushing and washing, and only the seeds were used. Green plastic seed trays (12 cm in diameter) with slits for drainage were put directly on the ground and fixed with a 8 cm long metal rod, which also bore a transparent 15×15 cm^2 perspex lid above the tray to reduce seed losses due to rain, wind and birds (for a more detailed description, see Kollmann et al. 1998). Two seed trays were placed in each of the 12 study quadrats, near the experimental plot for seed addition. Ten seeds per species were put in each tray, i.e. $2 \times 12 \times 10 = 240$ seeds per species, and in total $6 \times 10 = 60$ seeds per tray. Seed trays were loaded with seeds on 18 August 2006 (day 0) and seeds remaining were subsequently counted on day 1, 3, 7, 15, 31 and 63.

Statistical analyses

The results of the seed sowing experiment had a few non-zero data points (see below) and were not subjected to any statistical treatment.

The seed predation data were analyzed using generalized linear mixed-effects models (GLMM) via penalized quasi-likelihood approximation (Venables & Ripley 2002, Zuur et al. 2009), as implemented in the lmer function of the lme4 library (by D.M. Bates and D. Sarkar) for R ver. 2.4.1 (R Development Core Team 2005). A quasipoisson error distribution (and log link function) was used because it gave the best approximation of the variance structure of the data used. The use of GLMM allowed us to account for the repeated measures on the same seed trays. Thus, seed tray identity was used as grouping factors for the random effects. An overall model was constructed adding species identity as another random factor. The following variates were used as fixed factors: days from start of the experiment, land-use history (ex-arable or continuously forested), stand age, stand area, total forest area and the distance to ancient forest (Appendix 1). The most parsimonious model was identified by sequential backward elimination of fixed factors. Similar models were made for each of the six species in turn. In these, only tray identity was used as a random factor.

Results

Background regeneration

The present study focuses on seed sowing and seed predation, not on a quantitative description of differences in natural regeneration between the two land-use history types. Nevertheless, we present a brief survey of the natural regeneration of woody plants in the study system. The vegetation of the two plantation types differed in species composition and cover of saplings of woody plants in the herbaceous layer (Appendix 2). In continuously forested plantations *Acer pseudoplatanus* (< 1 m, 1–5 m) and *Quercus robur* (< 1 m) were common. In contrast, *Sambucus nigra* (< 1 m), and *Fraxinus excelsior* (of both height classes) were more common in plantations on ex-arable land.

Germination of sown seed

Seedling emergence was extremely sparse. No seedlings of *Alnus glutinosa* emerged, and very few of the remaining five species. Nine seedlings of *Rhamnus catharticus* emerged in four plots from a total of 360 seeds (2.5% recruitment success). For *Frangula alnus* and *Sorbus aucuparia* it was three and one seedling, respectively. No seedlings of the above species were found in the control plots. For *Sorbus intermedia* and *Sambucus nigra*, the number of seedlings emerging was identical (five and two, respectively) in sown and control plots.

Table 1. – Relationship of post-dispersal seed predation (SP) to forest history (continuously forested and ex-arable) and geographical factors. Results of generalized linear mixed-effects models (GLMM) in which species and tray identity are random factors. Only the first four non-null models are significant according to the log-likelihood test. Codes: *k* – number of terms included in each model; LL – model log-likelihood; ΔAIC – change in Akaike Information Criterion; ΔBIC – change in Bayesian Information Criterion; and %DE, percent deviance explained.

	k	LL	ΔAIC	ΔBIC	%DE
SP ~ NULL	2	–2008	0	0	0
SP ~ Day	3	–1420	1334	1330	32.0
SP ~ Day + History	4	–1413	1346	1336	32.3
SP ~ Day * History	5	–1295	1580	1566	38.0
SP ~ Day + Total forest area	4	–1414	1344	1335	32.3
SP ~ Day + Stand age	4	–1419	1334	1325	32.0
SP ~ Day + Stand area	4	–1420	1333	1323	32.0
SP ~ Day + Distance to ancient	4	–1420	1332	1323	32.0

Table 2. – Relationship of post-dispersal seed predation (SP) of the six forest species to forest history (continuously forested and ex-arable) and geographical factors in young oak plantations. Results of generalized linear mixed-effects models (GLMM) in which tray identity is a random factor. The best model for each species is presented. For abbreviations see Table 1.

Species	Best model	*k*	LL	ΔAIC	ΔBIC	%DE
Carex sylvatica	SP ~ Day + History	4	–134	243	236	47.9
Crataegus monogyna	SP ~ Day * History	5	–117	252	243	52.6
Frangula alnus	SP ~ Day	3	–157	539	536	63.2
Sambucus racemosa	SP ~ Day	3	–181	537	534	59.8
Sorbus aucuparia	SP ~ Day * History	5	–180	379	369	51.7
Viburnum opulus	SP ~ Day * History	5	–167	346	336	51.3

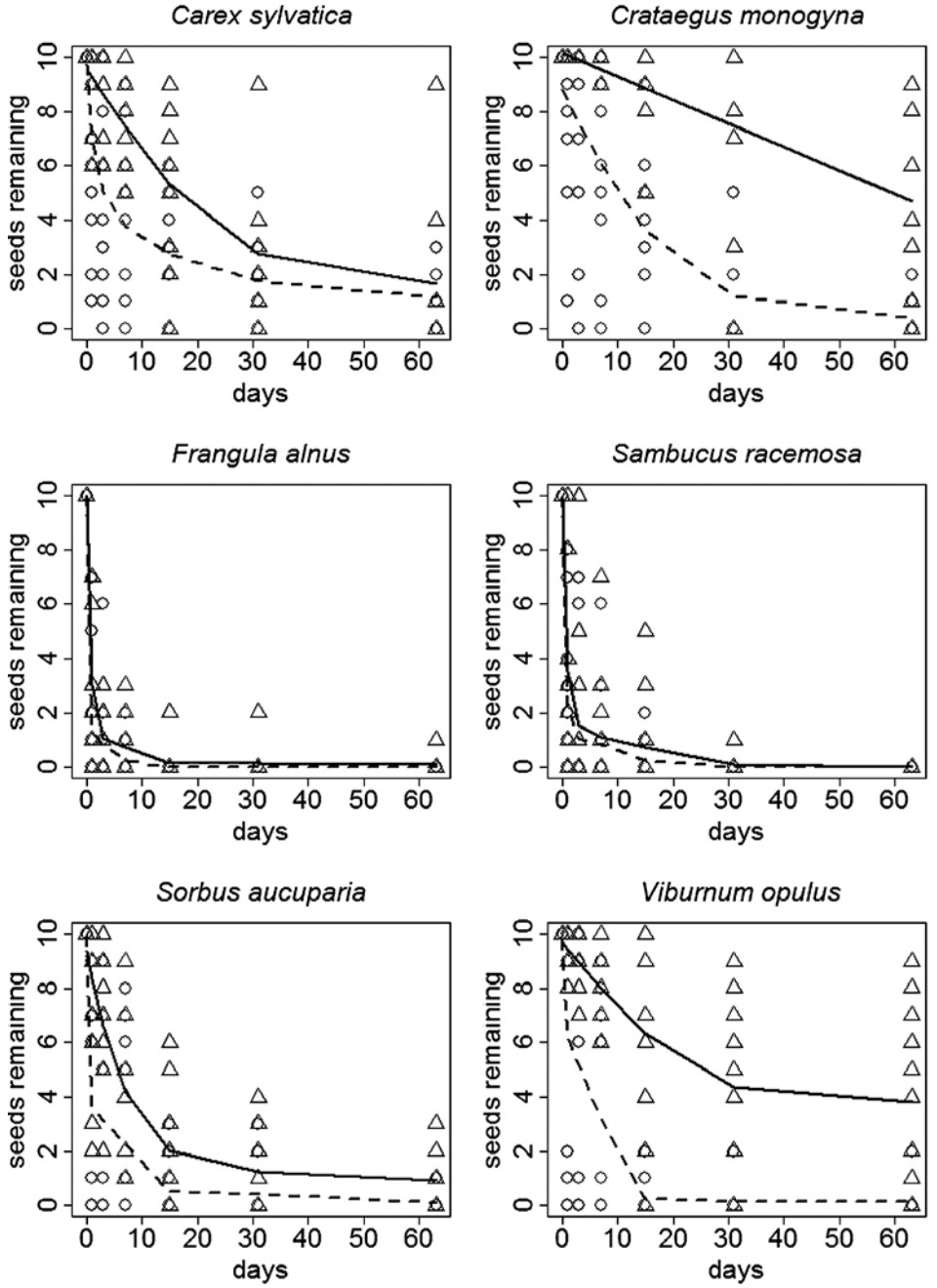

Fig. 1. – Post-dispersal predation of the seed of six forest species measured in terms of the numbers of seeds remaining in 24 trays after 1, 3, 5, 12, 28 and 60 days. Starting value was 10 seeds per tray. Complete lines and triangles indicate results for sites in continuously forested areas, dotted lines and circles sites on ex-arable land. Statistical significance of the differences between ex-arable and continuously forested site are given in Table 1.

Seed predation

Seed predation of all six species was intense, with most seeds disappearing within 1 day, and few remaining after 60 days. The GLMM for all species collectively (species identity used as a random factor) showed a significant difference in seed predation levels between ex-arable and continuously forested sites and an interaction between history and days from onset of the experiment (Table 1). The interaction term between day and land-use history accounted for a significant part of the variation in seed predation. Total forest area, which was highly correlated with site history, accounted for almost exactly the same information as land-use history. However, the interaction term between day and total forest area was not significant. Neither age or area of stand nor distance to ancient forest accounted significantly for variation in seed predation levels.

For four out of six species, there was a significant difference in seed predation rate between ex-arable and continuously forested sites (Table 2). *Crataegus monogyna* pomes disappeared more slowly at continuously forested sites than at ex-arable sites (Fig. 1), but fruits remained in the trays at ex-arable sites even after 60 days. Elevated predation rates in ex-arable plantations were also found for *Sorbus aucuparia Viburnum opulus* and *Carex sylvatica*. For *Frangula alnus* and *Sambucus racemosa*, seed predation was substantial (Fig. 1), but unrelated to any site factor, including plantation type (Table 2).

Discussion

There were marked differences in the spontaneous occurrence of seedlings and saplings of woody plant species in oak plantations on former agricultural land and those on continuously forested land. *Acer pseudoplatanus* was very abundant at continuously forested sites, but absent at sites on ex-arable land. The planted canopy species, *Quercus robur*, regenerated better at continuously forested sites than at sites on ex-arable land. In contrast, both seedlings and saplings of *Fraxinus excelsior* and *Sambucus nigra,* and seedlings of *Ulmus glabra* were more abundant at sites on ex-arable land. This may be attributed to their preference for the relatively high soil pH characteristic of ex-arable land (Valtinat et al. 2008).

The very poor recruitment in the seed addition experiment suggests that the habitat is strongly limiting for woody forest species colonizing woods planted on ex-arable land. This is the case for all the species investigated except *Rhamnus catharticus*, for which recruitment was better but dispersal could be a limiting factor. However, the nature of the habitat limitation was not discernible from the results. The rationale of sowing seed was to compare recruitment in sown and unsown plots in order to assess the degree to which dispersal is a limiting factor (Münzbergová & Herben 2005) and that at sites treated differently in order to assess the (micro)site factors limiting recruitment. However, many woody species have low per-seed recruitment rates (Clark et al. 1999) and the relatively small number of seeds sown in the present experiment greatly weakens any conclusions.

The most striking pattern is the marked difference in seed predation in continuous forest and forest plantations on ex-arable land. While a high incidence of post-dispersal seed predation in areas where there is canopy cover has previously been recorded (Kollmann & Buschor 2003, García et al. 2005), the results presented here indicate that colonization of recent forest plantations by woody forest species may be habitat-limited. This is surprising

because little seed is likely to be dispersed from old to new forests, and seed predation should only be of appreciable importance to plant population dynamics where seed is abundant (Andersen 1989). However, it is possible that the relatively high number of seeds in the experimental trays might have attracted predators and resulted in predation above the level of that experienced at more normal seed densities.

Predation of the seed of woody species was higher at ex-arable sites than continuously forested sites. The most likely cause of this is the influx of seed predators from the agricultural landscape matrix (Kollmann & Buschor 2003), which may completely surround forests on ex-arable land (on average ca 50% of stand border length), but not of continuously forested sites. However, it was not possible to separate the effect of land-use history from that of landscape configuration. Further investigations are needed to confirm this interpretation. Rodent faeces were found in very few of the seed trays, suggesting that rodents may not have been the main seed predators at all study sites, which contrasts with the findings of other investigations (e.g. Kollmann et al. 1998, Kollmann & Buschor 2003, García et al. 2005). Beetles and slugs were frequently observed in the empty trays, tentatively suggesting they may be implicated in the disappearance of seed. But again, trapping experiments are needed to directly identify the seed predators.

The predation pressure recorded at the study sites, with most of the seed disappearing from the trays within the first few days, is probably high enough to affect plant recruitment, although seed removal might not always lead to seed destruction. No cross-species comparisons were made, because presenting more than one species in each tray makes this very difficult.

Previous investigations report that the colonization of temperate forests by herbaceous plants, trees and shrubs is limited by their poor dispersal ability (Eriksson & Ehrlén 1992, Ribbens et al. 1994, Clark et al. 1998, Ehrlén & Eriksson 2000, McEuen & Curran 2004, 2006). The results presented suggest that high seed predation in forests bordering on to agricultural land may be responsible for the low recruitment. Further studies are a prerequisite for an increased understanding of how to create the optimal conditions in plantations for them to develop into species-rich forest.

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Souhrn

Opětovně zalesňované plochy na bývalé orné půdě v temperátních oblastech představují potenciální stanoviště pro lesní druhy. V bylinném patře těchto výsadeb však roste méně lesních druhů než v jinak srovnatelných výsadbách na stanovištích, kde bylo zalesnění kontinuální. Jedním z důvodů tohoto rozdílu může být omezené vzcházení lesních druhů. Tato práce se snaží pozorovaný rozdíl vysvětlit analýzou postdisperzní predace semen, především dřevin, v mladých dubových výsadbách v jižním Švédsku. První generace výsadeb na bývalé orné půdě byla srovnávána s opětovnou výsadbou na vykácených, kontinuálně zalesněných stanovištích. Při experimentálních výsevech šesti běžných druhů dřevin (*Alnus glutinosa*, *Betula pendula*, *Frangula alnus*, *Sambucus nigra*, *Sorbus aucuparia* a *Sorbus intermedia*) nebylo pozorováno žádné vzcházení, což svědčí o tom, že limitujícím faktorem při kolonizaci původními druhy keřů a stromů je stanoviště; jedinou výjimkou je *Rhamnus catharticus*, kde se zdá být důležitější limitace šířením. Postdisperzní predace byla významná, zejména v relativně malých a izolovaných výsadbách na bývalé orné půdě; to platí pro *Crataegus monogyna*, *Sorbus aucuparia* a *Viburnum opulus*, zatímco

u *Frangula alnus* a *Sambucus racemosa* nebyla ovlivněna polohou a historií výsadby. Tyto výsledky naznačují, že predace semen pravděpodobně limituje obnovu polopřirozených lesních porostů více, než se předpokládalo.

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Appendix 1. – Summary of site characteristics. History class: 1 – continuously forested; 2 – ex-arable.

Site ID	History class	Stand age 2005	Distance to edge of nearest ancient woodland (m)	Stand area (ha)	Total forest area in 1999 (ha)	Canopy species	Forest name
109g	1	66	0	6.63	1000	*Quercus robur*	Bökeberg
37g	1	49	0	1.75	759	*Q. robur*	Bokskogen, Rydskratt
56b	1	70	0	4.10	759	*Q. robur*	Bokskogen, Fäladsskogen
58a	1	53	0	4.00	759	*Q. robur*	Bokskogen, Fäladsskogen
163	1	58	0	1.20	759	*Q. robur*	Bokskogen, Torup
250	1	58	0	0.80	759	*Q. robur, Acer pseudoplatanus*	Bokskogen, Torup
12f	2	46	660	1.80	25	*Q. robur*	Gripskogen nord
17i	2	59	340	3.10	22	*Q. robur*	Gripskogen syd
23g	2	52	110	1.39	15	*Q. robur*	Skabersjö gård
28de	2	55	500	0.95	10	*Q. robur*	Svenstorp
42bn	2	62	170	1.24	14	*Q. robur*	Sönnarp
4d	2	70	1150	1.14	33	*Q. robur*	Västraby

Appendix 2. – Woody species regeneration at sites with different land-use history. Average percentage cover of woody seedlings and saplings (0–0.5 m height) and young trees (0.5–5.0 m, in parentheses) is given.

Species	Continuously forested sites	Ex-arable land
Abies alba	0	< 0.1
Acer pseudoplatanus	2.3 (5.8)	0 (0)
Betula pendula	0	0.1
Corylus avellana	0 (0.1)	0 (0)
Crataegus spp.	0.1 (0)	0.2 (< 0.1)
Fagus sylvatica	0.2 (1.8)	0.2 (1.5)
Frangula alnus	0.3 (0.5)	0 (0)
Fraxinus excelsior	0.4 (0.4)	7.7 (1.3)
Prunus padus	<0.1	0.1
Prunus spinosa	0	<0.1
Pyrus communis	0	<0.1
Quercus robur	1.6 (0.4)	<0.1 (0.5)
Sambucus nigra	0 (0)	1.8 (< 0.1)
Sambucus racemosa	0.2 (0.4)	0 (0.9)
Sorbus aucuparia	0.1	0.1
Tilia cordata	0	0.8
Ulmus glabra	< 0.1 (1.2)	2.2 (0)